ORIGINAL STRUCTURE AND COMPOSITION OF PERMIAN RUGOSE AND TRIASSIC SCLERACTINIAN CORALS

by JAMES E. SORAUF

ABSTRACT. Rugose corals from the Permian of Timor (Indonesia) and scleractinian corals from the Triassic of northern Italy are both exceptionally well preserved. The scleractinians, as shown previously by Montanaro Gallitelli, are preserved as the original aragonite. They have skeletal structures virtually identical to those in living corals, with some minor diagenetic alteration but without change in mineralogy. Microprobe scan lines show strontium as the common minor element in the Triassic skeletal aragonite. The rugosans studied were selected as the best-preserved available Permian corals, from Basleo, Timor. Small crystal sizes within calcitic skeletal micro-structure and perfect development of trabecular septal structure, as shown by scanning electron microscopy in polished and etched sections and also in broken sections, suggest little diagenetic alteration in some specimens. Where diagenetic structures are recognizable (as in walls of *Polycoelia*) they are obviously discordant with primary biogenic structures. Skeletal carbonate with little or no observable diagenetic alteration at the electron microscopic level is lacking in both strontium and magnesium as minor elements, suggesting that low magnesian calcite, rather than aragonite was the primary skeletal mineral composition in these Permian corals.

RESULTS of a comparative study of the structure and composition of Permian and Triassic corals are presented here. The question to be answered is whether there was originally a great difference between Permian rugose corals and early scleractinian corals. Palaeontologists, carbonate petrologists, and geochemists are all concerned with possible differences in coral structure and mineralogy and, by inference, with possible differences in metabolic processes or protein chemistry or sea-water chemistry. A number of authors have commented on this question, but the opinion has almost always been based merely on the apparent quality of preservation of fossil corals; the only exception is the work of Lowenstam, who reported on the composition of several rugose corals (1963, p. 187).

In order to make meaningful statements regarding mineralogy, composition, and possible recrystallization, one must first, know a reasonable amount regarding diagenetic processes that may have been operative during the history of burial and fossilization, and second, both understand rather precisely the formation and patterns of biogenic structures in the coral skeleton in living and fossil scleractinians, and also have empirical data regarding the microstructure of the rugosan skeleton. This includes the means of assessing structures as to their biogenic origin or later development due to diagenetic alteration of carbonates. Such information is here used in the comparison of very well-preserved Upper Permian (Guadalupian) corals from the island of Timor with exceptionally well-preserved Late Triassic (Carnian) corals of northern Italy (text-fig. 1). The primary sources of this data are the scanning electron microscope and the electron microprobe.

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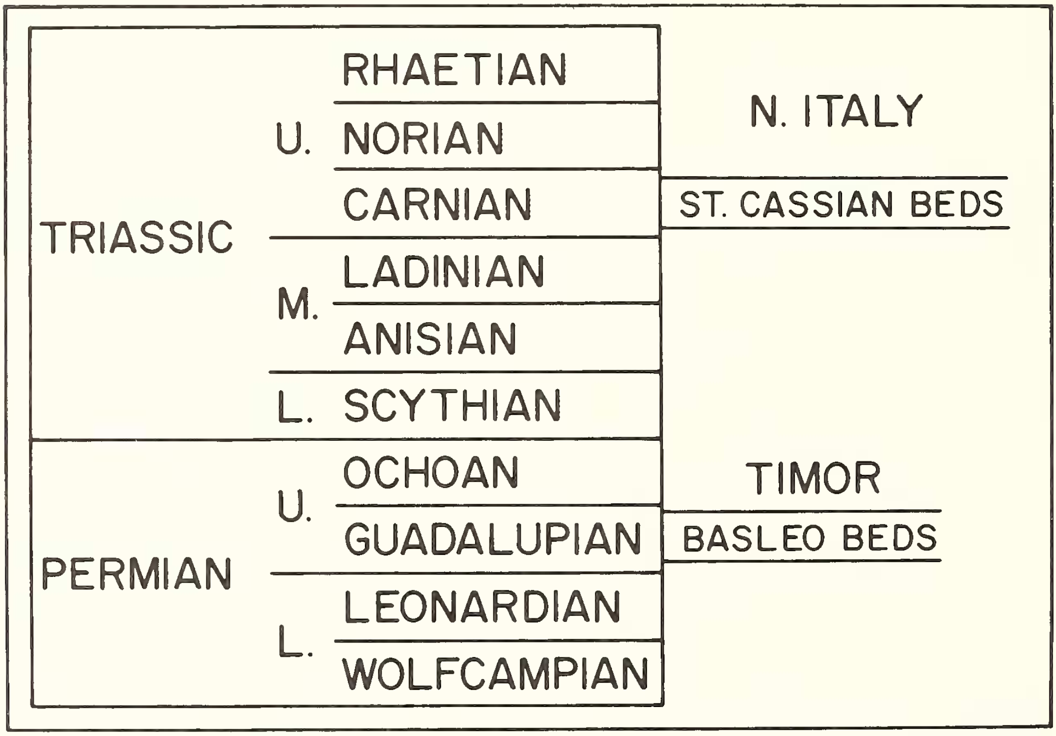
MATERIAL

The Permian fossils from the island of Timor are justly famous for their excellent preservation and are also of great interest due to the variety and make-up of this late Palaeozoic fauna. As one can note in the published literature, especially on the photographic plates of Schindewolf (1942), details of coral skeletal structures are excellently preserved. A few exceptionally well-preserved Permian specimens were thus chosen during a visit to the Geologisches-Paläontologisches Institut at the Friedrich Wilhelm University at Münster, which houses a large collection of Permian corals from Timor. These were collected by J. Wanner during expeditions in 1909 and 1911 and have been recently studied by Schouppé and Stacul (1955, 1959) and by Nierman (1975). The specimens that are reported on here are all from the Basleo 23 collecting locality.

Aragonitic Triassic scleractinian corals have been reported from northern Italy by Montanaro Gallitelli (1973, 1974) and studied taxonomically and for their microstructure. Her fauna, collected from near Cortina d'Ampezzo has also been studied for strontium content in some detail by Montanaro Gallitelli, Morandi, and Pirani (1973). The specimens included in the present study were collected by the writer at the 'Sett Sass' locality (Ogilvie Gordon 1929, p. 399). The specimens were determined by X-ray



TRIASSIC	U.	RHAETIAN	N. ITALY
		NORIAN	
		CARNIAN	ST. CASSIAN BEDS
	M.	LADINIAN	
		ANISIAN	
	L.	SCYTHIAN	
PERMIAN	U.	OCHOAN	TIMOR
		GUADALUPIAN	BASLEO BEDS
	L.	LEONARDIAN	
		WOLFCAMPIAN	

TEXT-FIG. 1. Permian and Triassic stages, with chronostratigraphic position of the St. Cassian strata from the Dolomiti and the Basleo beds of Timor.

diffraction to be aragonite, and have provided data on the location of minor elements and microstructure of exceptionally well-preserved scleractinian corals to compare with the Permian corals of Timor.

Illustrated specimens are in one of two repositories. The Triassic specimens from this paper are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and the Permian specimens are in the Geologisches-Paläontologisches Institut, Münster (G-PMM).

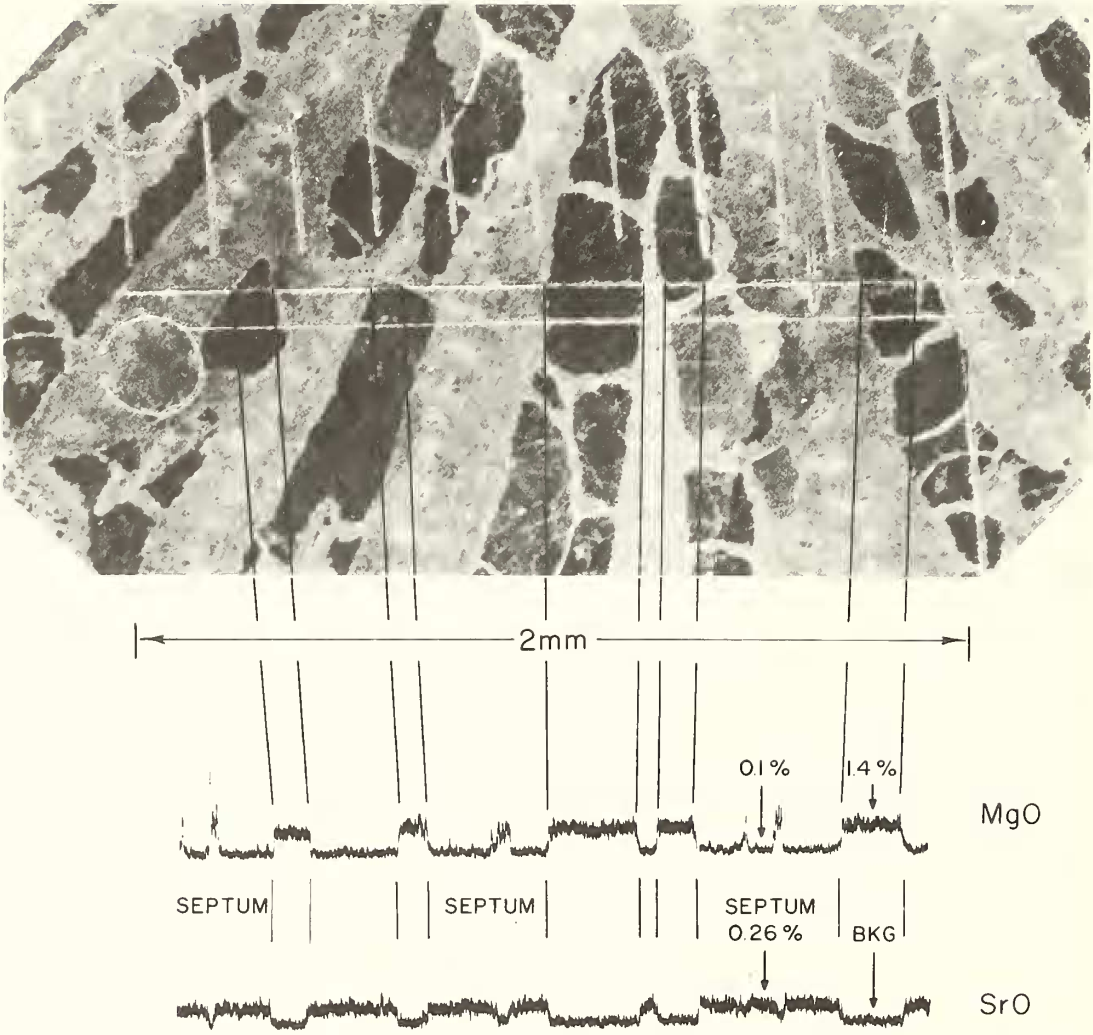
METHODS OF INVESTIGATION

This study attempts to locate precisely the distribution of minor elements in the skeletal carbonate and in interskeletal void-filling carbonate. Thus, specimens selected for intensive study were first thin-sectioned and one sawed surface was then polished for study with the electron microprobe. After polishing, lines were scribed for the traverse path and for a scale, utilizing a centred diamond stylus mounted in place of an objective lens on a metalographic microscope. After the microprobe traverse had been run, analysing for strontium and magnesium, the specimen was lightly etched for study in the scanning electron microscope. This light etch not only retained the scribe markings for scale and path, but also etched into visibility the microprobe traverse line (text-fig. 2), where carbonate has been partially destroyed by the electron beam. In addition, skeletal and interskeletal carbonate has been variably etched, so that biogenic elements can be easily differentiated from the calcitic spar filling interseptal spaces. This system allowed for exact correlation of data from microprobe scan lines and individual elements of each coral. After correlation, the specimens were polished lightly once again to remove traces of scribed lines, and then etched with 0·1 normal formic acid for study of structures within the scanning electron microscope.

It should also be noted that some of the Permian specimens from Basleo are so well preserved that they could be successfully studied in broken sections by means of the scanning electron microscope. Small crystal sizes and an apparent lack of recrystallization allow detailed study of skeletal structure by this method, which has not been of value in the study of Palaeozoic corals.

TRIASSIC SCLERACTINIAN CORALS

Triassic corals were collected by me from the St. Cassian strata (Carnian Age) during visits to the Dolomiti of northern Italy (1961, 1975). The collections were made from brownish shales where they overlay the famous dolomitized Richthofen Reef (Ogilvie Gordon 1929, p. 399). This is the locality referred to as 'Forcella di Sett Sass' by Volz (1895, p. 100). Of a number of corals collected by me from this locality, one colony of *Thecosmilia*, apparently that named *T. badiotica* by Volz (1895, p. 26) was chosen for detailed microprobe analysis and scanning electron microscopy. Further microscopy was carried out on biogenic structures in a colony of *Isastraea* cf. *I. gumbeli* Laube 1865. Both specimens have skeletal elements composed of aragonite, as shown by X-ray diffraction.



TEXT-FIG. 2. *Thecosmilia badiotica* (USNM 245274). Composite micrographs to show septa, dissepiments, and spar filling former void spaces. Scribed lines show the start (with a circle), path, and finish of the scale and traverse line, marked by a long bar. The microprobe traverse line has been etched into prominence, lies between the scribed lines, and can be identified by the black lines drawn to it from below. Below are noted traverse elemental scan lines for magnesium and strontium, as well as semi-quantitative analyses at the points shown. Note that each septum is marked by a line of trabecular centres which also make themselves evident in the microprobe analysis by their anomalous content of magnesium and strontium.

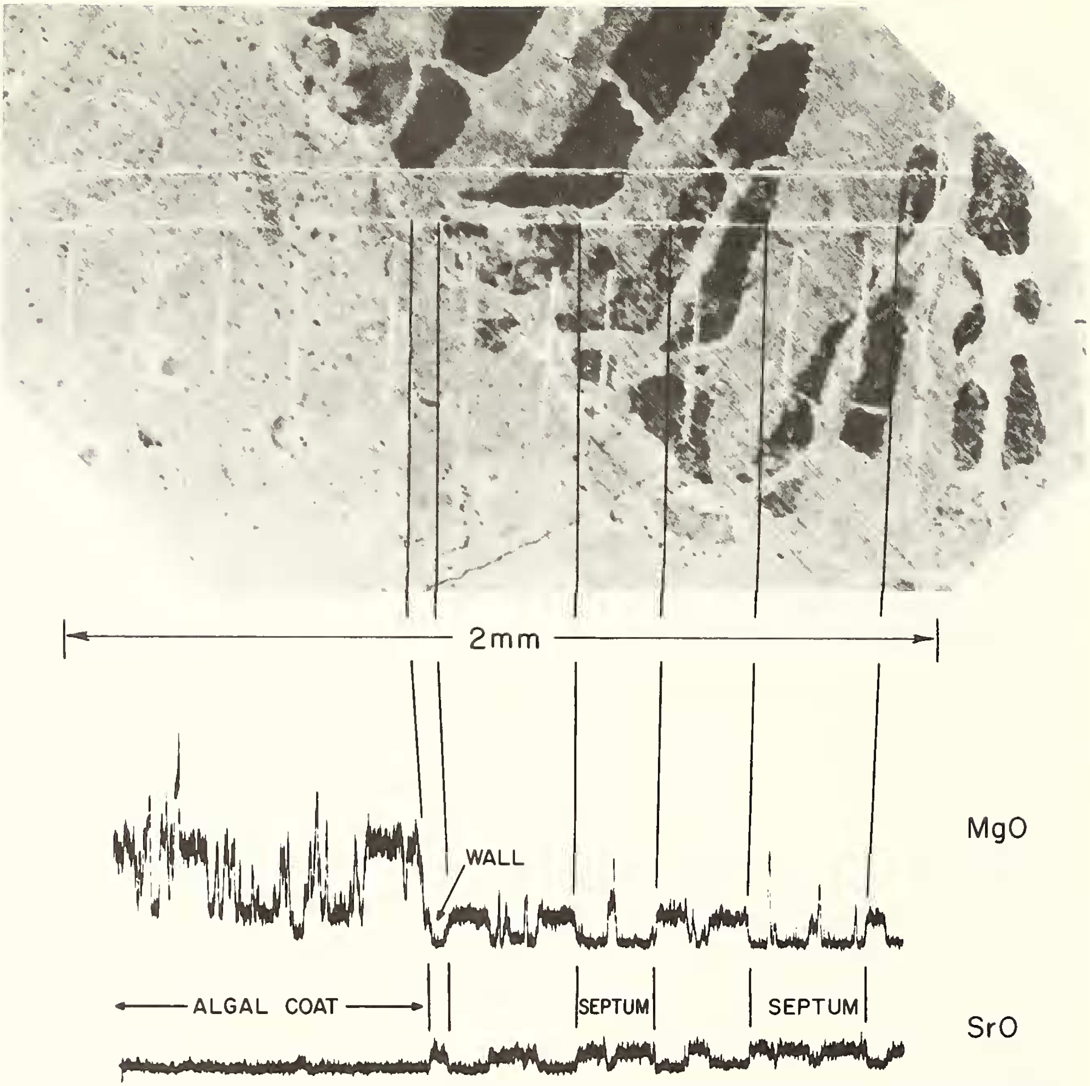
Thecosmilia badiotica Volz

This specimen of *Thecosmilia* is part of a large colony. Unfortunately, the thin-section is just within a budding sequence (Pl. 30, fig. 1) and is thus elongate and difficult to recognize as that form referred to as *T. badiotica* by Volz (1895, p. 26). Microprobe traverses were run in two widely separated areas and the area, the trace, and the analysis for each is shown (text-figs. 2 and 3). As can be seen in the first of these figures, the etched surface shown in the scanning electron micrograph (SEM) clearly differentiates between skeletal carbonate and the sparry infilling (calcitic) between skeletal elements. The skeletal aragonite and sparry calcite are mirror images with respect to the occurrence of magnesium and strontium, with the skeletal aragonite being relatively high in SrO (approx. 0·25% by weight) and reading at background count to show the absence of magnesium. The calcitic spar is as high as 1·4% MgO by weight by reading at or close to background for strontium content. It is also noticeable here that spikes occur in the minor element contents in the centres of the septa. This suggests strongly that these trabecular centres of the septa are altered. As was noted for Pleistocene corals from Barbados, alteration of septal aragonite commonly commences at the centres of the finely crystalline septal trabeculae (James 1974, p. 790). Text-fig. 3 is another composite SEM with correlative microprobe traces, with the scan line (probe) beginning in a calcitic algal coating of the corallite and progressing into the corallite interior. Here it can be seen once again that the skeletal aragonite contains strontium, that the sparry calcitic infilling has some magnesium, but much less than that of the calcitic algal coating, and what are apparently recrystallized trabecular centres show as spikes on the microprobe traverse for MgO as it crosses the septum.

The same surface, repolished and re-etched prior to study in the scanning electron microscope, provides evidence on the structure of skeletal features in this Triassic coral. The septa are finely trabecular (in thin-section view showing the central 'dark line') with good preservation of trabecular centres (Pl. 30, fig. 2), and within trabecular centres there are small radiating crystals as well as evidence of some small amount of recrystallization (Pl. 30, fig. 3). Dissepiments likewise show a feature characteristic of modern corals with crystal growth from the bordering septa to a centre line, with a junction groove (Sorauf 1970, p. 7) shown on the undersurface of the dissepiment (Pl. 30, fig. 4).

That portion of wall coated by algal calcite is shown (when repolished and re-etched, Pl. 30, fig. 5) to be composed of typical thin stereotheca composed of spherulitic clusters, expanding towards the centre of the corallite and with the axis of the cluster perpendicular to the outer margin of the wall (Pl. 30, fig. 6). The lower part of this micrograph shows a rather large amount of randomly distributed material (apparently organic debris) in the algal coating. Endolithic algae have also apparently bored into the wall of this *Thecosmilia*, so this Triassic coral not only has a perfectly modern skeletal structure but is also associated with modern-looking algae.

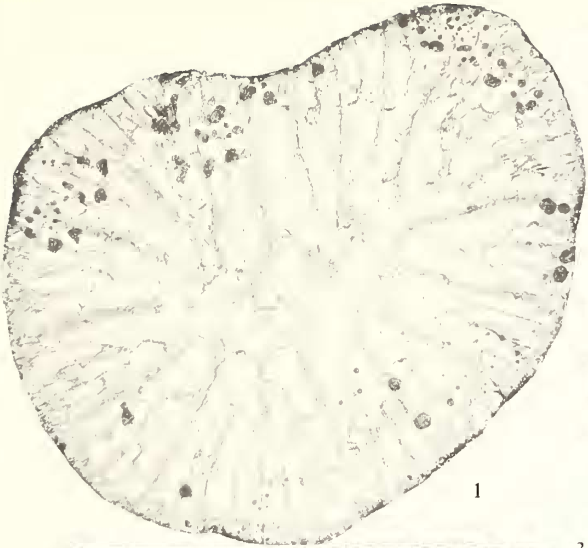
In some septal cross-sections, this specimen of *Thecosmilia* does show slight effects of recrystallization, predicated by James's model and also shown by magnesium content in microprobe traverses. This recrystallization of trabecular centres (Pl. 30, figs. 2 and 3) is most likely reflecting susceptibility to solution of very fine crystallites in trabecular centres.



TEXT-FIG. 3. *Thecosmilia badiotica* (USNM 245274). Composite micrographs showing line of electron microprobe as for text-fig. 2. Here the traverse line begins at the left in a coating of algal calcite, passes into the corallite through the wall, and traverses septa and interseptal carbonate. Note again that trabecular centres are visible in the septa and are also marked by anomalous amounts of MgO and SrO.

EXPLANATION OF PLATE 30

Figs. 1–6. *Thecosmilia badiotica* Volz (USNM 245274). 1, transverse view in thin-section (of specimen about to bud), × 10. 2, scanning electron micrograph (SEM) longitudinal to corallite axis, transverse to septum showing trabecular centres with little alteration of central crystals, × 400. 3, SEM enlargement of centre of septal trabecula from septum in fig. 4, illustrating minor recrystallization of fine aragonite crystallites to calcite, × 2000. 4, SEM transverse to dissepiment with central junction groove on basal surface (arrow), × 400. 5, SEM providing overview of septa and algal material shown in text-fig. 3, after repolishing and re-etching, × 50. 6, SEM enlarging portion of fig. 5, to show theca with crystal clusters and axis of clusters perpendicular to outer surface of wall, coated with algal calcitic mass (arrow at junction). Note also scattered whitish organic debris in algal coating, × 500.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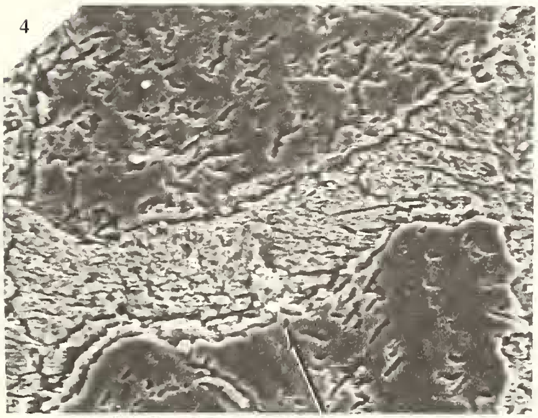
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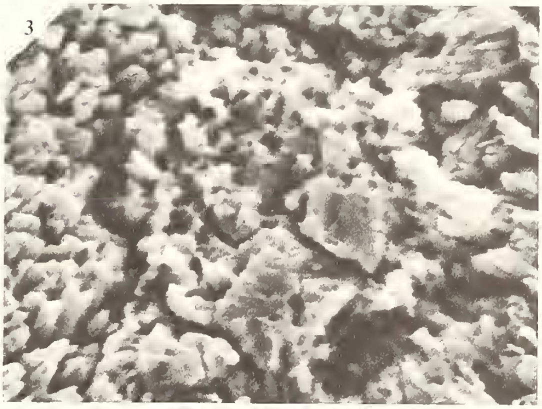
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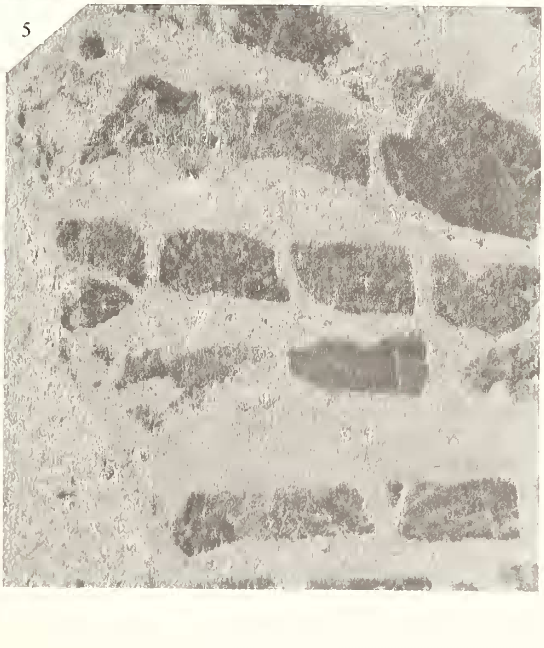
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SORAUF, coral structure

Isastraea cf. *I. gumbeli* Laube

Although no chemical analyses have been made on *Isastraea* cf. *I. gumbeli*, some structural studies are presented here which provide further evidence of the modern appearance of these corals. In longitudinal thin-section, the large septal trabeculae are clearly shown, along with some inorganic aragonitic overgrowths on flanks of septa (Pl. 31, fig. 1). In SEMs of polished and etched sections of septa, trabeculae appear to be large, with well-marked centres, and form dentation apparent on the proximal margin of the septa (Pl. 31, fig. 2). Micrographs of dissepiments as cut transversely in a section longitudinal to the corallite axis show two characteristic features, the upward growth of crystals in the main portion of the dissepiments, and the widespread occurrence and modern appearance of endolithic algae (Pl. 31, fig. 3).

PERMIAN CORALS

The Permian corals from Timor have been studied the same way as the Triassic scleractinians, as noted previously. Three genera are reported on, *Polycoelia*, *Timorophyllum*, and *Lophophyllidium*, with the greatest emphasis on the first two.

It is here noted that useful studies could be made on broken sections of *Polycoelia* and *Timorophyllum*, with results comparable to those obtained by study of Recent corals in broken section. This is the first time that such studies have been successful on Palaeozoic corals, and attests to the splendid preservation of these specimens.

Polycoelia angusta Rothpletz

P. angusta is a small, solitary rugose coral characterized by bilateral symmetry, thick stereotheca and septa with the axial ends expanded (Pl. 31, fig. 4). It can be seen in thin-section that the fine structure shows axial ends of the septa inflated by incremented growth, with dark growth lines clearly visible within this part of the septum. Here trabeculae are strongly inclined axially and the main crystallite growth is (at the tip) laterally orientated towards the axis of the corallite (Pl. 31, fig. 5). The zigzag structure is variably developed within the walls of this specimen.

In a microprobe scan line run across five septa and intervening interseptal spar, it is immediately noted that the SrO content counts are at the background level of the

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EXPLANATION OF PLATE 31

Figs. 1–3. *Isastraea* cf. *I. gumbeli* Laube (USNM 245275). 1, longitudinal thin-section of septal trabeculae, slightly oblique to plane of section, showing preservation of what are apparently aragonitic overgrowths on trabeculae (arrow), × 36. 2, SEM longitudinal to septum near crest, illustrating large trabeculae with well-marked centres (arrow) and trabecular denticulations on septal crests, × 400. 3, illustration of transverse section of dissepiment, polished and etched, to show upward growth of crystals and presence of endolithic algae (arrow), × 500.

Figs. 4, 5. *Polycoelia angusta* Rothpletz (G-PMM-B2.399). 4, transverse section of small corallite, with typical symmetry and septa with inflated axial tips, × 10. 5, enlargement of axial end of long septum at right-hand side of fig. 4, here showing fibrous crystal structure and incremental growth lines, plane polarized, × 75.

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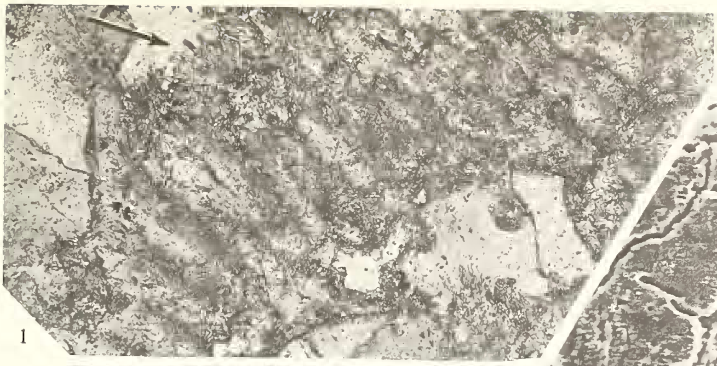

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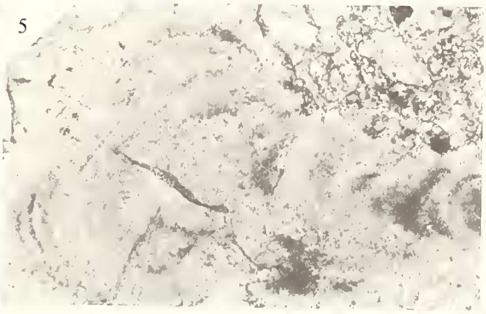
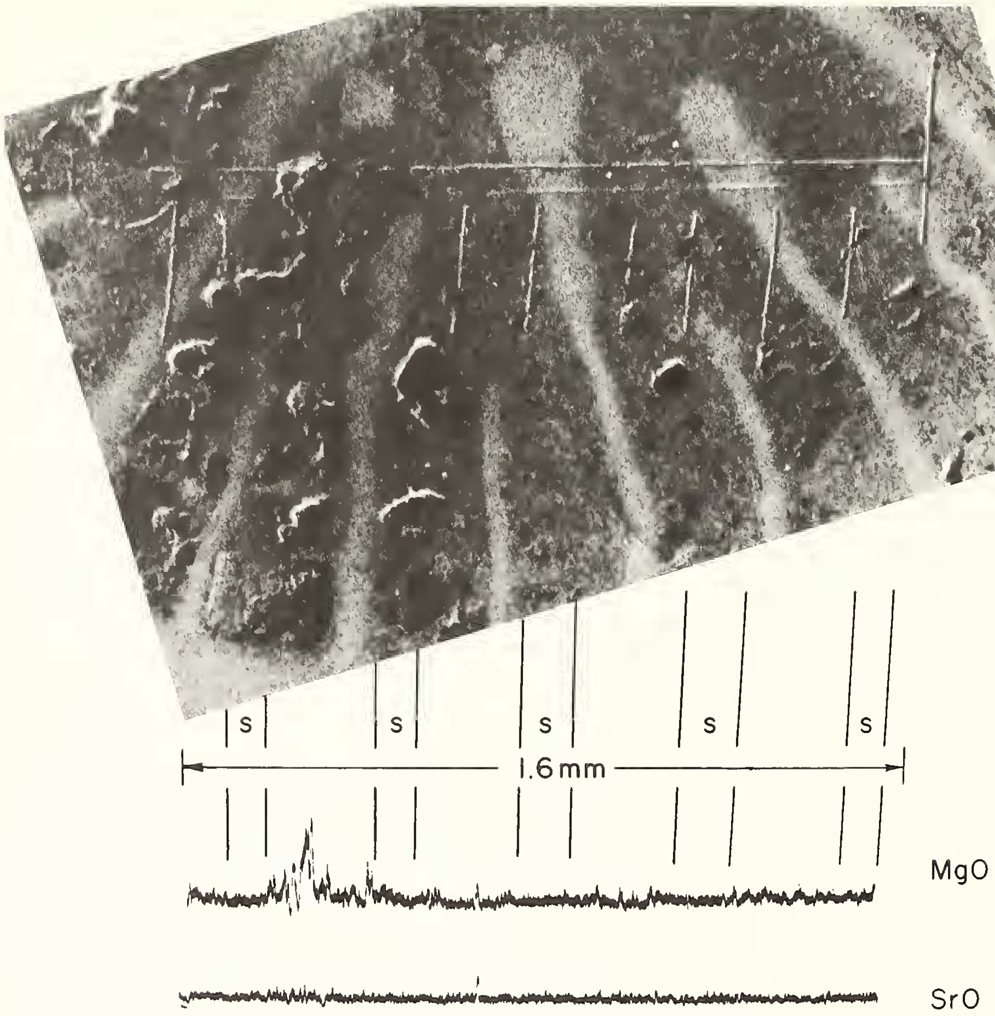


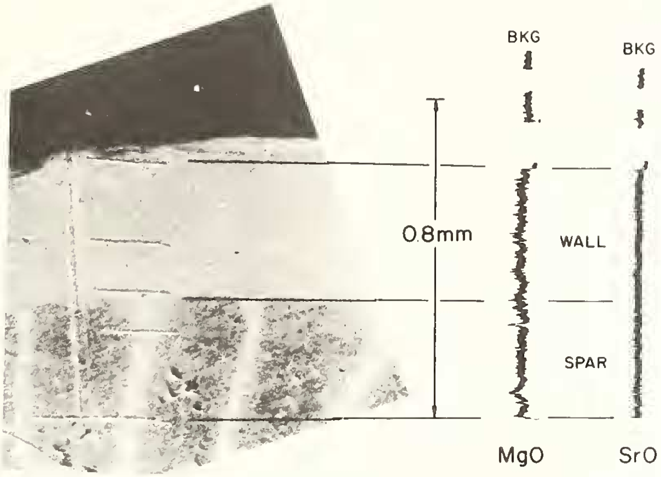
SORAUF, coral structure



TEXT-FIG. 4. *Polycoelia angusta* (G-PMM-B2.399). Composite micrographs of traverse across septa of *Polycoelia* as in text-fig. 2. Note that there exists little or no difference in MgO content between septa and spar. The peak near the left side of the MgO line corresponds with topographic irregularity shown above on the scan line and is apparently a result of the hole at the surface of the sample.

instrument (text-fig. 4), and that the MgO distribution is not markedly different between septa and spar, although the magnesium distribution curve is perhaps somewhat more uniform (fewer pertubations) in some septa. However, as the greatest character in the MgO count is produced by surface irregularities (text-fig. 4), it is entirely possible that the only variations noted in this curve are the result of variation in the perfection of the surface polish. Certainly the minor element content of the calcitic septa is not markedly different from that of the interseptal spar. When these same septa were repolished and re-etched (Pl. 32, fig. 1), the specimen shows the truly magnificent preservation of the septa, with the axial tip of the septum characterized by extremely small crystals, with growth lines visible on the scanning micrograph (Pl. 32, fig. 1).

The wall of the corallite was likewise analysed for minor element distribution by a line of traverse perpendicular to the outer surfaces of the wall (text-fig. 5). Here again, little magnesium is noted and the strontium content is apparently near zero. This analysis of the wall was made specifically to obtain bearing on the so-called zigzag wall structure, present in some of the thick-walled specimens of the Timor fauna, first discussed by Schindewolf (1942, p. 36). This microprobe data is totally inconclusive except to reinforce the opinion that the wall is here similar in composition to the interseptal spar infilling the corallite.



TEXT-FIG. 5. *Polycoelia angusta* (G-PMM-B2.399). Composite of scanning micrograph of outer portion of corallite showing wall, septa, interseptal spar, and scale and traverse line as in text-fig. 2. Note that there is no difference apparent between the MgO content of wall and of spar.

This same specimen, when repolished and more fully etched, illustrates quite well the zigzag appearance of the wall structure seen in transverse section (Pl. 32, fig. 2). However, in the same micrograph can be seen a septum inserted in the wall. The orientation of the crystals within the septum bears no obvious relation to the orientation of crystals within the wall. That this septum is very well preserved is illustrated by its remarkable appearance in the broken section of the tip of the septum (Pl. 32, fig. 3). The crystal structure can be seen just as on the polished and etched section, here not only with divergent crystals but also with remarkably small crystal sizes in the centre of the septum. A broken section of the wall shows the cause of the zigzag structure. This section (Pl. 32, fig. 4) shows a generally transverse section, but a third dimension is also clearly visible. It is in this direction, longitudinal to the corallite, that recrystallization (perhaps coupled with directed pressures) has formed crystals greatly enlarged in the vertical direction, forming large lath-like crystals that are deformed so that when cut in transverse section they clearly show the zigzag form. The very large size of these crystals, apparently recrystallized, lends further credence to the proposed diagenetic origin for this structure (Oekentorp 1974; Sorauf 1977). A view of the septum discussed earlier (Pl. 32, fig. 5) shows that it is fine-grained, with divergent crystals all the way to the junction with the area of recrystallized calcite (the wall), with no apparent continuity of the structure across this boundary. This clearly suggests that the wall has been greatly modified since formed and that the septum has at the same time remained almost totally unchanged.

Timorophyllum wanneri Gerth

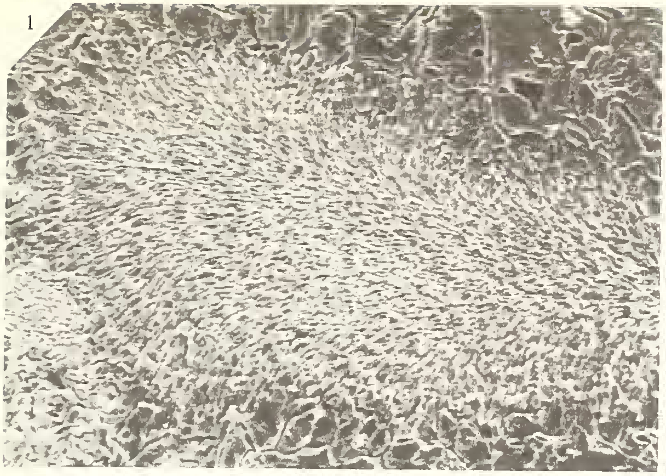
T. wanneri is a medium-sized solitary coral (diameter of 1·0–1·2 cm) characterized by a columella which imparts a definite bilateral symmetry to the corallite in transverse section (Pl. 33, fig. 1). The fine structure of the septa as seen in transverse section shows a central dark line with crystallite growth out perpendicularly towards the flanks of the septa. Crystal growth in the walls is likewise perpendicular to the outer surface of the wall, with septa having an inserted appearance into the wall (in this figure, the characteristic is somewhat exaggerated by solution at this boundary). Under higher magnification, the dark line is seen as a line of fine crystals connecting septal trabeculae, also with small crystals in the trabecular centres. This same specimen, analysed for MgO, shows that there is a significantly smaller amount of magnesium in the septa than in the interseptal spar (text-fig. 6) and also that the septa are quite uniform in their composition. The spar is apparently more variable in magnesium distribution, but it is not possible to quantify this, owing to surface irregularities in the polish of this part of the specimen.

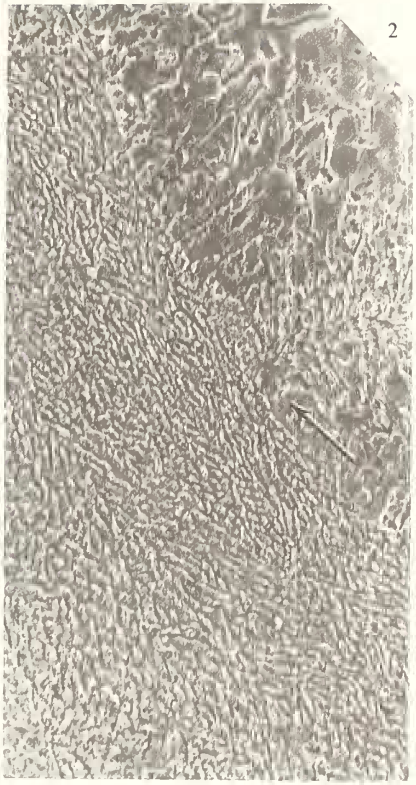
Although there is an appreciable difference in composition between septa and spar in this specimen of *Timorophyllum* another equally well-preserved specimen (Pl. 33, fig. 2) does not show this. In this microprobe traverse of this well-preserved septum (text-fig. 7), there is no difference apparent between the septal calcite and the sparry calcite, and the data would seem here to be inconclusive.

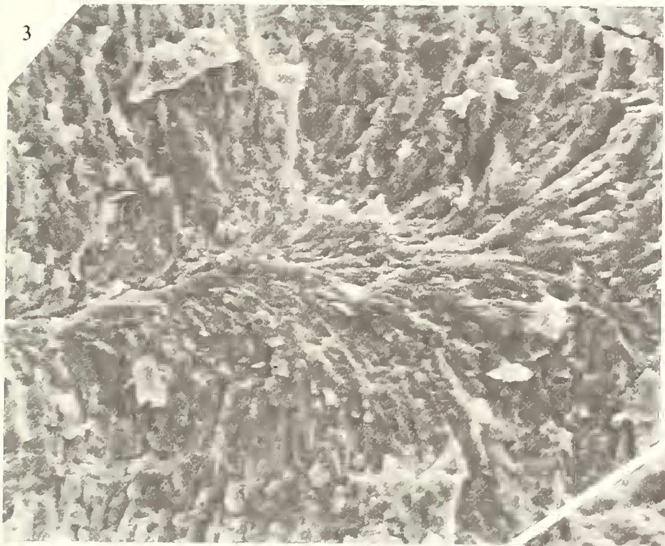
EXPLANATION OF PLATE 32

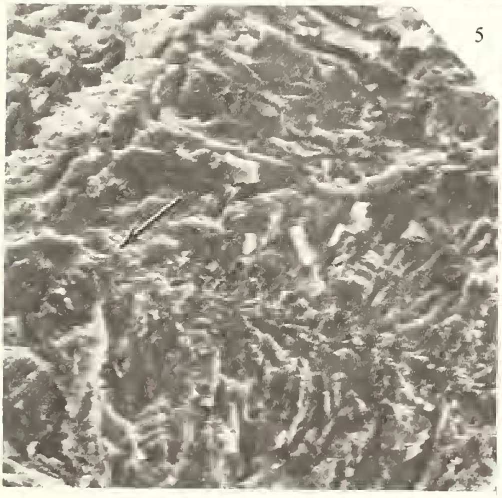
Figs. 1–5. *Polycoelia angusta* Rothpletz (G-PMM-B2.399). All scanning electron micrographs (SEM). 1, enlargement of tip of septum, illustrating fine diverging crystals and visible growth lamellae, × 200. 2, zigzag structure in same wall illustrated in text-fig. 5, here repolished and re-etched. Here, in transverse section, no relation is seen between the structure of the wall and that of the septum (arrow) at right, × 200. 3, transverse view in broken section across septum, illustrating small diverging crystals, just as in polished and etched section (Pl. 32, fig. 1), × 500. 4, broken section of wall with upper portion of micrograph showing transverse section of wall (arrow) but with third dimension illustrating elongation of large crystals in the longitudinal direction, with their junctions providing zigzag structure, × 1000. 5, broken section of wall and dissepiment showing non-congruency of structure at junction of the two (arrow), × 500.

PLATE 32

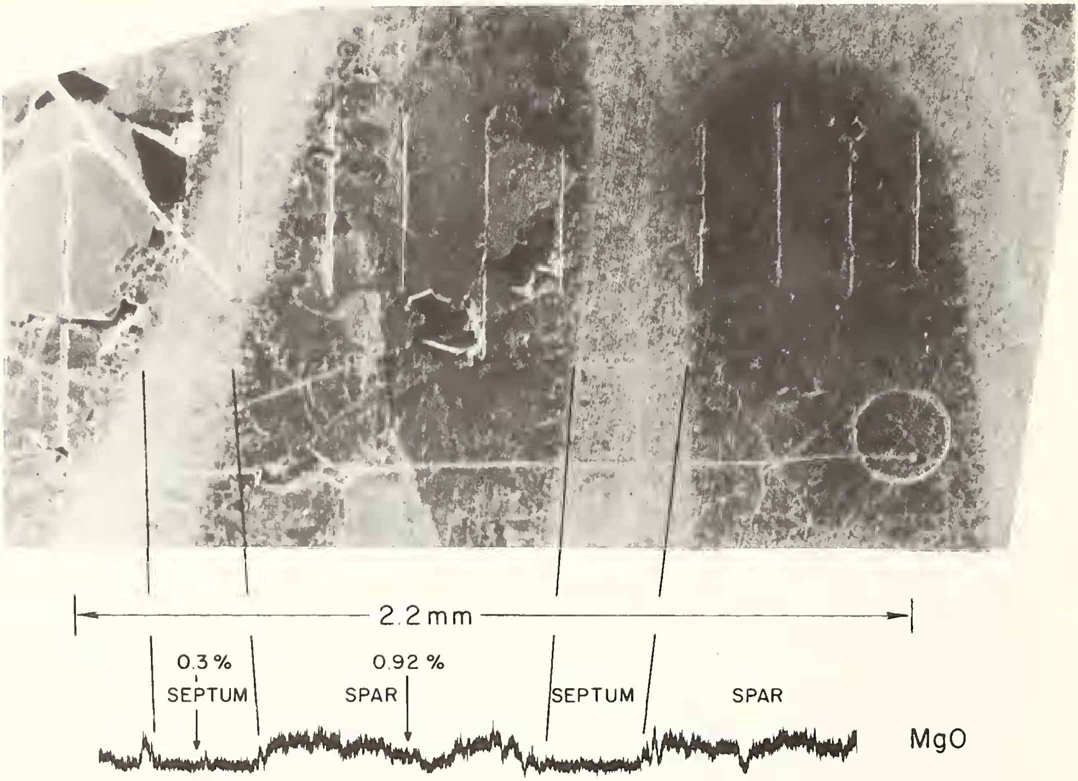








SORAUF, coral structure



TEXT-FIG. 6. *Timorophyllum wanneri* (G-PMM-B2.400). Composite micrographs illustrating position of microprobe scan line as shown by lines drawn from MgO printout line to trace of scan line after light etching, as for text-fig. 2. Note that septal calcite has a lower MgO content than does interseptal spar. The weight percentages of MgO are approximate only.

EXPLANATION OF PLATE 33

Fig. 1. *Timorophyllum wanneri* Gerth (G-PMM-B2.400). Transverse view of corallite showing columella, symmetry, and central dark line to septa, and crystal growth perpendicular to margins of both wall and septa.

Fig. 2. *Timorophyllum wanneri* Gerth (G-PMM-B2.401). SEM transverse to tip of septum showing very well-delineated septal trabeculae, and crystal overgrowth extending structure, × 400.

Figs. 3–5. *Lophophyllidium spinosum* Martin (G-PMM-B2.402). 3, transverse view illustrating columella and remarkable quartz crystal overgrowths on elongate septa, × 7·5. 4, enlargement of portion of previous view showing acicular quartz crystals and clear centres to septal trabeculae, × 25. 5, SEM of polished and etched transverse section of septum with silicification duplicating radiating crystal structure of septal trabeculae, × 200.

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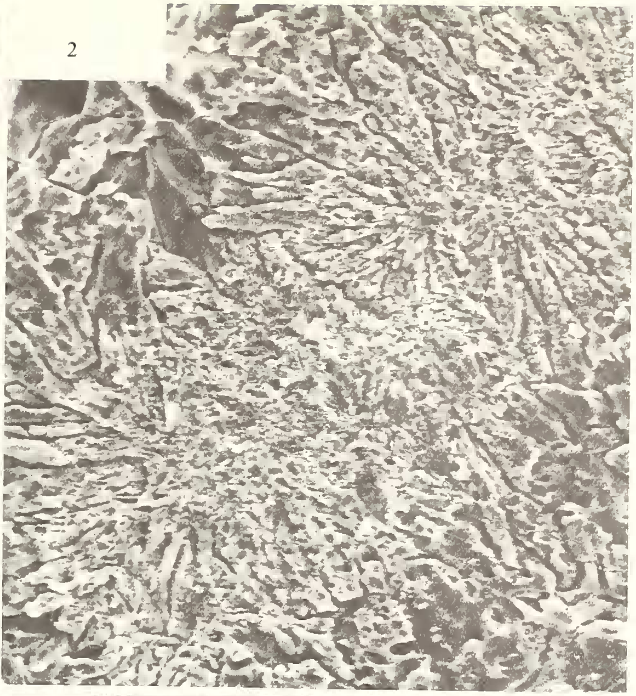

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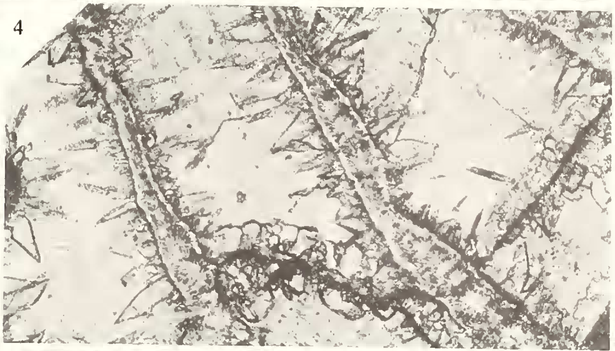

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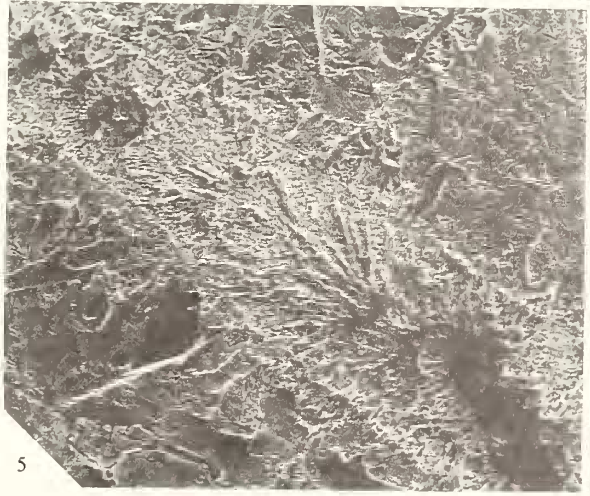
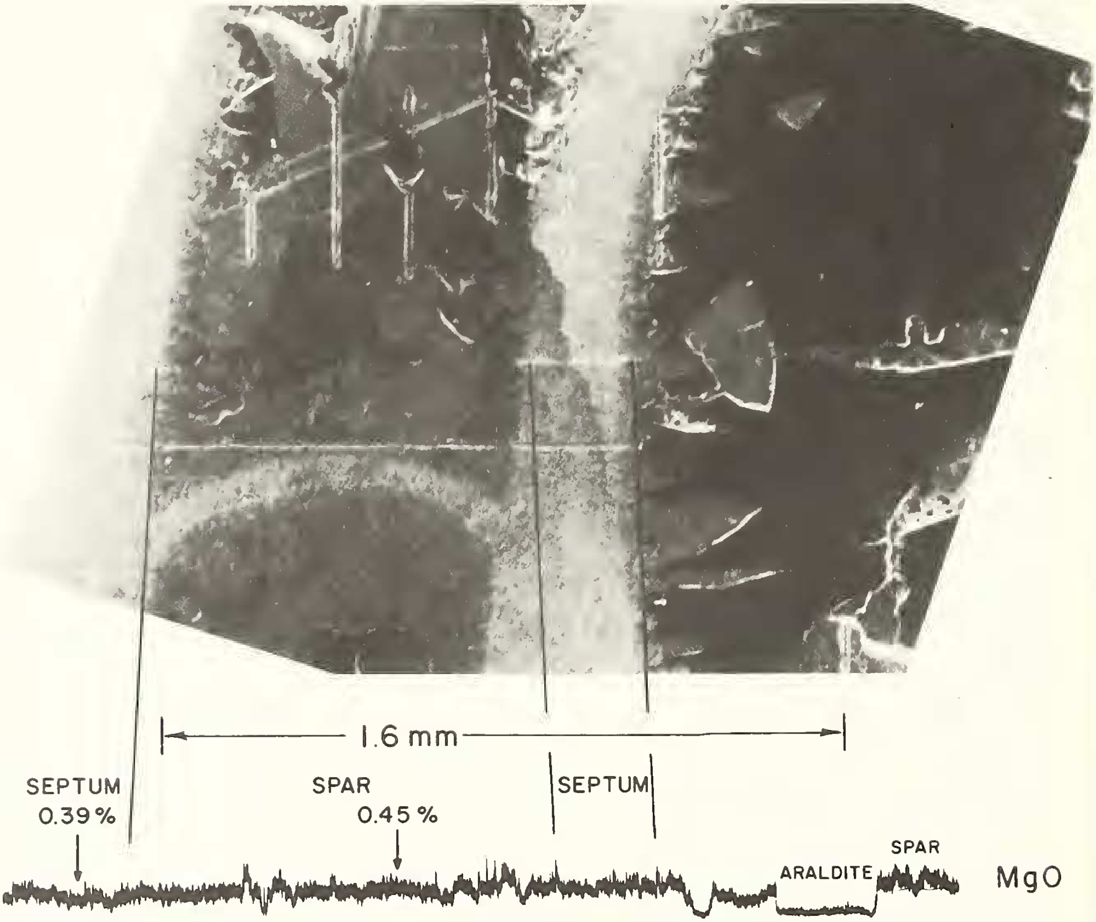


SORAUF, coral structure

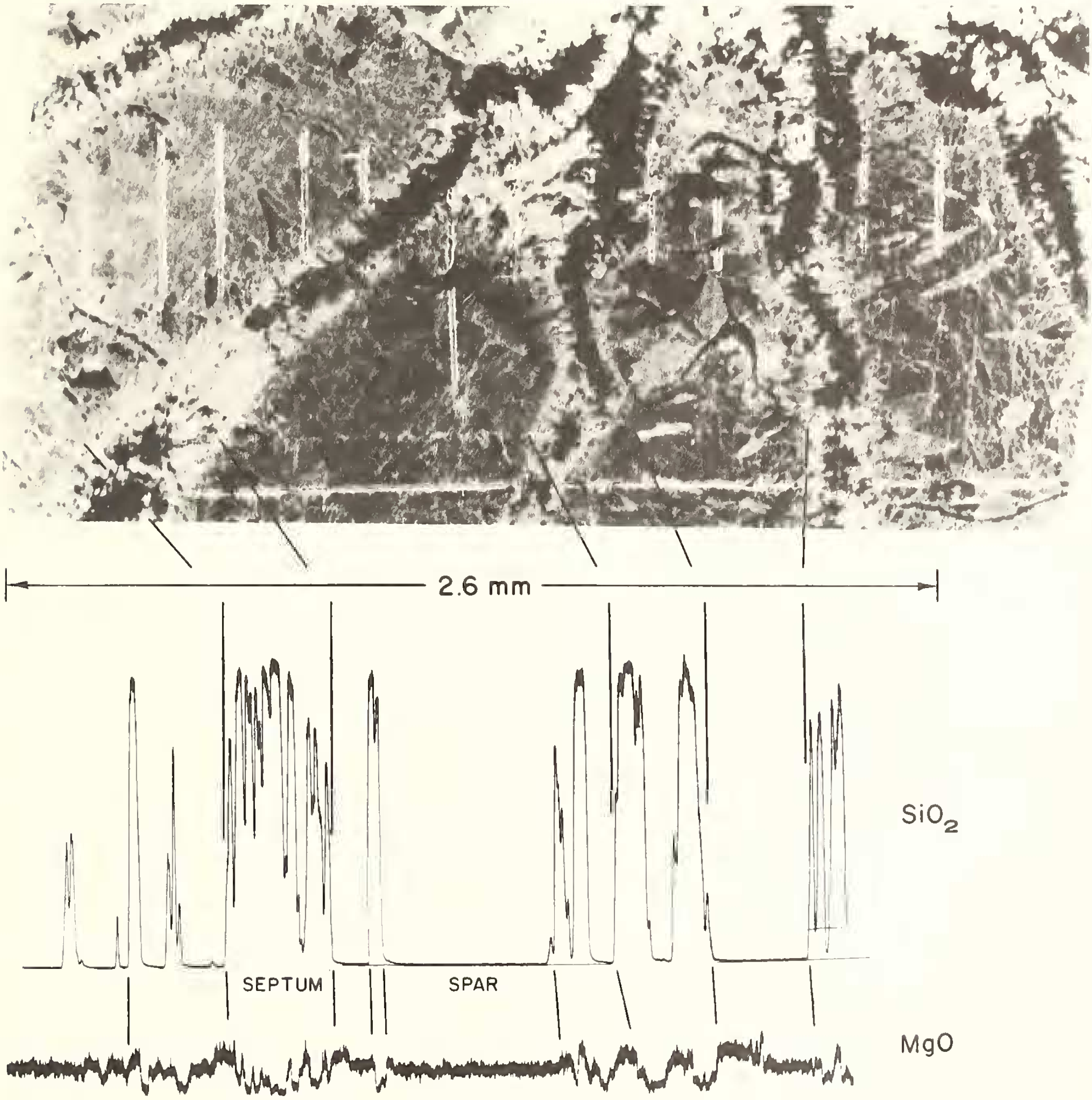
Lophophyllidium spinosum Martin

A single partially silicified specimen of *L. spinosum* was examined for structure and chemistry. This *Lophophyllidium* is characterized by long thin septa and prominent columella (Pl. 33, fig. 3). Although not immediately apparent, this specimen is partially altered (Pl. 33, fig. 4), although the fine structure of the septa has not been greatly altered: trabecular centres can be seen rather clearly in this photomicrograph. A microprobe traverse across several septa does indeed show major amounts of silica, especially in the trabecular centre at the left side of this micrograph (text-fig. 8). Repolishing and re-etching of this septum shows clearly the preferential silicification of the trabecular centres (Pl. 33, fig. 5) and indeed, preferential silicification of crystals radiating from the centres. This is a peculiarity which has not previously been reported



TEXT-FIG. 7. *Timorophyllum wanneri* (G-PMM-B2.401). Composite micrographs illustrating path of MgO scan line, as in text-fig. 2, after a light etch. Septa are here very much the same as interseptal spar with regards to magnesium content.

from other corals, either rugosans or scleractinians. The evidence is slight, and further data should be collected before making a more detailed hypothesis. I suspect, however, that the silica is replacing unrecrystallized carbonate and duplicating biogenic structures. This type of incipient silicification (or other diagenetic processes) starts at centres of trabeculae, just as calcitization of modern aragonitic corals begins at the centres of trabeculae where the crystals are smallest.



TEXT-FIG. 8. *Lophophyllidium spinosum* (G-PMM-B2.402). Composite micrographs to show position of microprobe scan lines as in text-fig. 2. Note that a close correspondence is seen between occurrence of silica and magnesium. It can also be noted here that silica is replacing trabecular centres of septa preferentially.

CONCLUSIONS

Late Triassic aragonitic corals are among the first-known scleractinians; their structure and minor element content is very like that of Recent corals (as shown for strontium by Montanaro Gallitelli, Morandi and Pirani 1973). Diffusion, if actually a factor affecting minor element distribution in carbonates, has apparently been of equal importance in lowering relative amounts of strontium and magnesium, not only in skeletal aragonite, but also in interseptal calcite spar.

Permian corals from Timor are among the best-preserved rugosans known. This fact, noted in thin-sections and in SEMs of polished and etched sections, is reflected to a remarkable degree in the septal structures and trabeculae noted in broken sections of both *Polycoelia* and *Timorophyllum*. The fact that crystal sizes noted in broken sections of trabeculae are not much different than those seen in trabeculae of modern corals is considered convincing evidence that little recrystallization has taken place in the skeletal carbonate.

Minor element analysis shows that negligible amounts of strontium and magnesium are present. This is in contrast with some data (Richter 1972; Sorauf 1977) that rugose corals had an elevated magnesium content in skeletal calcite. In the Timor specimens there is no apparent, consistent difference between composition of the spar and the composition of the skeleton.

The sole identifiable diagenetic fabric ('structure') noted is the zigzag seen in the wall of *P. angusta*. This wall makes an abrupt and discontinuous contact with the septa, which are still exceptionally well preserved. The diagenetic structure was recognizable in part because of the very large size of the crystals relative to those within the septal trabeculae, reinforcing the hypothesis that septal calcite is not recrystallized in these specimens.

Early stages of silicification of *L. spinosum* show a concentration of silica in centres of septal trabeculae, with this replacement process replicating the septal microstructure rather faithfully. This suggests that the silica was replacing unrecrystallized calcite. It is also important to note that the region of replacement is the same as in the vadose calcitic replacement of Pleistocene scleractinians. In both cases, replacement is first in the very fine-grained grained centres of trabeculae.

Diagenetic structures such as zigzag features are (to me) unknown in any post-Palaeozoic corals. I would infer that they are diagenetic structures developed in biogenic calcite but not in aragonite replaced by calcite. The remarkable preservation of skeletal structures in calcitic Permian corals at the electron microscopic scale, and the completely different minor element chemistry suggest that the Rugosa originally had a skeleton of calcite, just as the Scleractinia have always had a skeleton of aragonite. This is likely to be the result of biological factors (protein chemistry, enzymal activity), rather than a reflection of external environment.

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JAMES E. SORAUF

Department of Geological Sciences and Environmental Studies
State University of New York
Binghamton, New York, 13901
U.S.A.

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